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# A population study of moorland Collembola

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With 9 figures in the text

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## 1. Introduction

Little information exists on the ecology of Collembola or Springtails of British uplands, and in the present paper information is provided on the Collembola of a moorland area in the northern Pennines, namely the Moor House National Nature Reserve, Westmorland, England.

Numerically the Collembola usually take second place only to the Acari, or mites, in the air-breathing fauna of the soil, and on occasions they have been found to be even more numerous than the mites (Stöckli 1943, 1946). Probably as a result of the frequency with which they are found in soil samples, there is an extensive literature on the group, although in Great Britain few ecological studies have been made. MURPHY (1955), who worked on the Moor House Reserve before the present study was begun, and HALE (1963) have provided the only ecological information available concerning the ecology of Collembola of high moorland in Great Britain, although JACKSON (1928) and MACFADYEN (1952) dealt with the fauna of fen land, which has a similar soil type and plant cover.

The Moor House collembolan fauna is made up mainly of species of Arthropleona and in the present work all the members of the Symphypleona are grouped. The species with which the present paper is concerned are as follows:

<i>Hypogastrura scotica</i> (CARPENTER and EVANS 1899)	<i>Folsomia quadrioculata</i> (TULLBERG 1871)
<i>Hypogastrura denticulata</i> (BAGNALL 1941)	<i>Folsomia manolachei</i> BAGNALL 1939
<i>Willemia anophthalma</i> BÖRNER 1901	<i>Folsomia cf. brevifurca</i> (BAGNALL 1949)
<i>Friesea mirabilis</i> (TULLBERG 1871)	<i>Folsomia litsteri</i> BAGNALL 1939
<i>Brachystomella parvula</i> SCHÄFFER 1896	<i>Isotomiella minor</i> (SCHÄFFER 1896)
<i>Anurida pygmaea</i> (BÖRNER 1901)	<i>Isotoma sensibilis</i> (TULLBERG 1876)
<i>Anurida forsslundi</i> (GISIN 1949)	<i>Isotoma notabilis</i> SCHÄFFER 1896
<i>Anurida granaria</i> (NICOLET 1847)	<i>Isotoma viridis</i> BOURLET 1839
<i>Neanura muscorum</i> (TEMPLETON 1835)	<i>Isotoma antennalis</i> (BAGNALL 1940)
<i>Onychiurus absolini</i> (BÖRNER 1901)	<i>Isotoma olivacea</i> TULLBERG 1871
<i>Onychiurus procampatus</i> GISIN 1956	<i>Isotoma infusca</i> (MURPHY 1959)
<i>Onychiurus latus</i> GISIN 1956	<i>Isotomurus palustris</i> (MÜLLER 1776)
<i>Onychiurus tricampatus</i> GISIN 1956	<i>Entomobrya nicoleti</i> (LUBBOCK 1867)
<i>Tullbergia krausbaueri</i> (BÖRNER 1901)	<i>Entomobrya multifasciata</i> (TULLBERG 1871)
<i>Tullbergia affinis</i> BÖRNER 1902	<i>Willowsia buski</i> (LUBBOCK 1869)
<i>Tullbergia denisi</i> (BAGNALL 1935)	<i>Lepidocyrtus cyaneus</i> TULLBERG 1871
<i>Tetracanthella wahlgreni</i> LINNANIEMI 1911	<i>Lepidocyrtus lignorum</i> FABRICIUS 1775, GISIN 1964
<i>Tetracanthella brachypura</i> BAGNALL 1949	<i>Pseudosinella alba</i> (PACKARD 1873)
<i>Folsomia brevicauda</i> AGRELL 1939	<i>Tomocerus minor</i> (LUBBOCK 1862)

Due to the advances in the taxonomy of the Collembola generally, and the revised species concepts applied to certain groups, it is often difficult or impossible to make comparisons with the published data of many of the earlier workers; however, this is done wherever possible. In this paper nomenclature of Collembola follows GISIN (1960); soil nomenclature follows the classification of KUBIENA (1953).

## 2. The study area and sampling sites

### 2.0. General remarks

The Moor House National Nature Reserve (N. R. 80) is located in the northern Pennines, ten miles south of Alston, Cumberland, although the Reserve itself lies in Westmorland. General descriptions of the reserve have been made by CONWAY (1955), NICHOLSON (1957), SVENDSEN (1957), COULSON (1959) and CRAGG (1961).

Four main sampling sites were selected which were typical of the major habitats found on the Reserve; these were as follows:

### 2.1. The Heather litter site

The soil profile was that of a typical Dystrophic Peat Ranker. The site was situated on an expanse of blanket bog where *Calluna vulgaris* was the dominant plant. At the base of the vegetation the peat was covered by a layer of *Calluna* litter which facilitated the cutting of good soil cores. The pH ranged from 4.5 to 4.9.

### 2.2. The *Juncus squarrosus* site

The soil type on this site was referable to a Peat Anmoor and the site itself was situated on shallow peat at the edge of the blanket peat, a typical moor edge zone. The pH varied from 4.5 to 4.6.

### 2.3. The Limestone grassland site

The soil type was referable to a Eutrophic or Mesotrophic Braunerde. The depth of the soil rarely exceeded 50 cm due to the bedrock being close to the surface. The pH varied from 4.9 to 6.6.

### 2.4. The Alluvial grassland site

The azonal soil on this site was a mixture of peat and mineral particles. The vegetation was very similar to that of the Limestone grassland but there were no lichens, whereas *Cladonia rangiferina* was found commonly on the Braunerde. The pH ranged from 4.5 to 6.0.

## 3. Methods

### 3.1. Extraction techniques

Methods of removing micro-arthropods from soil samples have been reviewed in KEVAN (1955) and these can be divided into two main categories. Firstly, there are those which rely on the movement of the animal along a physical gradient such as heat, desiccation or light, the so-called "automatic" methods and, secondly, there are the mechanical methods involving sieving or flotation, where the animals are extracted independent of their own activity. Initially the second type of extraction technique was discarded as unsuitable for organic soils such as those encountered in this study; however, later during this work a flotation method was developed for the removal of arthropods from organic soils (HALE 1964).

MACFADYEN (1953, 1955, 1961) has described and compared several methods of extracting soil arthropods from soil samples. At the time when the present work was begun a high gradient extraction apparatus had been developed which proved to be up to ten times as efficient as an ordinary Tullgren funnel (MACFADYEN 1961); this type of extractor was used for the present work.

Several modifications of the procedure recommended by MACFADYEN (1961) were found to be necessary. Due to the number of samples taken, and the frequency with which different areas were sampled, it was found that the five day period recommended was too long for an apparatus of only 32 units. Two extractions a week were required and due to this the period of extraction was reduced to three days. It was also found that the recommended heat gradient of 20 °C over the depth of the soil sample did not dry it out completely. With the relatively low temperature of 20 °C at the lower surface of the sample unit, *Collembola* remained in it even after a five day extraction, if it was not completely dried out. It was eventually decided that a three-stage extraction would be the best; for the first twelve hours of the extraction the transformer (Zenith Variac Type 100 M) was set at 60 volts; after 12 hours it was set at 100 volts for 24 hours and then at 160 volts until the sample dried out, a period which varied between 12 and 24 hours depending

Table 1 Temperature gradients during a three day extraction

Time from beginning extraction (Hours)	Variac reading (Volts)	Temperature of cooled side of soil sample (°C)	Temperature of heated side of soil sample (°C)
0	60	19.0	19.0
12	60	19.0	34.0
13	100	18.5	55.0
20	100	19.5	58.5
25	100	18.8	58.5
36	100	18.8	55.5
37	140	21.0	76.0
48	140	20.0	79.0
60	140	20.0	80.0

upon the soil type. Table 1 shows the temperatures, read by a mercury thermometer, which corresponded to the transformer readings.

Due to the short period of extraction it was found unnecessary to use fixatives and fungicides in the canisters, and the animals extracted were not killed until the extraction was complete, when 70 % alcohol was added to the water in the canisters.

Because of the size of the apparatus and the fact that the sample units were divided into two horizontal layers, when 30 sample units were taken half had to be stored for a period of three days before extraction; this was also the case when two sets of 15 units each were taken. It was found that storing in a refrigerator at 4 °C for a period of three days had no significant effect on the extraction.

### 3.2. Sampling

Since it was required to estimate the variations in numbers of the commoner species in addition to the total numbers of Collembola, a sample unit size which would yield numbers in the order of 20—200 individuals was sought. A sample unit size of  $\frac{1}{1000}$  m<sup>2</sup> was finally decided upon and cores were taken to a depth of 6 cm.

In the construction of the sampler it was found necessary to use Tufnol cores which gave a surface area of more than  $\frac{1}{1000}$  m<sup>2</sup>, as tubing of exactly the right diameter could not be purchased. The surface area of the sample units taken was 11.35 cm<sup>2</sup>. A sampler was designed to take Tufnol cores of the type described, and its construction was essentially similar to that described by MACFADYEN (1961). Sample units of 3 cm or 6 cm in depth were normally taken and this involved the use of one (3 cm) or two (6 cm) Tufnol rings. The rings were inserted into the sampler where they were held by means of a retaining cylinder clamped in place by a lid. Samples were taken at random by throwing the containers of Tufnol rings and sampling one metre from the top of the container, along its axis.

MACFADYEN (1957) recommended 30 sample units where the distribution of the organisms is patchy and a unit size similar to that chosen here. Initially during the course of this work 30 sample units were taken each month on several soil types. The period between sampling dates was decided on the basis of what was known of the life cycles of Collembola, not more than two or three generations a year being expected at Moor House. Throughout the greater part of the study 15 sample units were taken each month, but in certain months more sample units were taken to provide more material.

The present paper provides information obtained from an analysis of the data from the following samples:

1. Limestone grassland: monthly samples on 24 occasions (February 1960 — December 1961). On the first six occasions 30 sample units were taken and subsequently 15 sample units. The analysis is of 450 sample units.

2. Alluvial grassland: monthly samples on 13 occasions (May 1960 — May 1961). On the first two occasions 30 sample units were taken and subsequently 15 sample units. The analysis is of 225 sample units.

3. Heather litter: monthly samples of 15 units on 13 occasions (January 1961 — December 1961). The analysis is of 193 sample units.

4. *Juncus squarrosus* grassland: 15 sample units were taken on four occasions over a period of one year. The analysis is of 57 sample units.

The number of sample units used in the analysis is on some occasions smaller than the number collected; this is due to accidental damage to the sample units during the extraction process.

When a soil core was removed from the sampler it was placed, together with the Tufnol ring retaining it, in an aluminium container. The sample was taken back to the laboratory in this way and the first extraction was normally started within six hours of collecting. The sample units to be extracted later were stored at 4 °C until required.

When loading the soil cores into the extractor 6 cm cores were cut in half by means of a knife; the upper surface (i. e. the upper surface in relation to the original orientation in the

field, but lower surface during extraction) of the 3—6 cm part of the core was scratched to counteract the effect of sealing the pores caused by cutting with a knife.

### 3.3. The sorting and counting process

Each canister removed from the high gradient cylinder extractor contained the Collembola from one core 3 cm deep. Alcohol was added to the water in the containers and the Collembola were thus preserved for counting. For counting purposes the contents of each can were poured into a petri dish of 10 cm diameter, the bottom of which had been squared in centimetres using a diamond pencil. The Collembola were systematically removed from the dish by means of a minute spatula, and the whole area of the dish was examined twice.

## 4. Results

### 4.1. Horizontal distribution

#### 4.1.1. Aggregations

ANDREWARTHA and BIRCH (1954) have pointed out that most animal populations are distributed non-randomly, and tend to patchiness rather than over-dispersion in their distribution. ELTON (1949) has stated that no habitat is homogeneous and clearly lack of, homogeneity of the habitat is likely to be reflected in the patchy distribution of animals. Thus, in a habitat as heterogeneous as the soil, patchiness is to be expected in the distribution of the animals living in it. Studies on the horizontal distribution of micro-arthropods have shown this to be the case. GLASGOW (1939), MACFADYEN (1952, 1957), RAW (1956), HUGHES (1962), KACSMAREK (1960), HAARLOV (1960), POOLE (1961), and MILNE (1962) have all found that micro-arthropods tend to be aggregated in the soil.

Since the present work was not primarily designed to produce information on the spatial distribution of Collembola, the only data available are from random sampling. No information on the size and possible distribution of aggregations can be derived from this, but an analysis is useful since no information of this type exists for the Collembola of moorland soils.

#### 4.1.2 The importance of the sample unit size

Sample units may be either too large or too small to show the presence of aggregations within a population; that is to say a given sample unit may contain more than one aggregation or only a single individual (or none). Thus, there exists for any population an optimum sample unit size for detecting aggregation. GREIG-SMITH (1952) has emphasised the importance of the quadrat size in studying the distribution of plants, and by random throws of coloured discs has shown that a single quadrat size is not sufficient to determine the randomness or otherwise of the distribution of a species. COTTAM et al. (1957) have also emphasised that any consideration of aggregation must be closely tied to the question of the area of the sample unit involved.

Whilst a given sample size may indicate that the individuals within a population are distributed randomly, following a Poisson expectation, this may not necessarily be the real state of affairs. However, if a given sample size detects aggregation this is a real phenomenon, and aggregations exist between individuals.

#### 4.1.3. The detection of aggregation by random sampling

##### 4.1.3.1. The Coefficient of Dispersion

SALT and HOLICK (1946) introduced Fisher's Coefficient of Dispersion into their analysis of the distribution of wireworm populations. The coefficient may be expressed by the following formula:

$$\text{C. D.} = \frac{\sum (x - \bar{x})^2}{\bar{x} (n - 1)} \text{ or } \frac{s^2}{\bar{x}}$$

where  $x$  is the number of individuals from each sample unit,  $\bar{x}$  is the mean value of the sample units and  $n$  is the number of sample units;  $S^2$  is the variance. This ratio is, in fact, that of the variance to the mean; when this is equal to unity there is a random or Poisson distribution; when it is greater than unity there is aggregation or under-dispersion and when it is less than unity there is an even distribution or over-dispersion.

The significance of the divergence of the coefficient of dispersion from unity is regarded as significant if it exceeds:

$$1 \pm 2 \sqrt{\frac{2n}{(n-1)^2}}$$

where  $n$  is the number of sample units. In this work, where samples of 15 units were used, the value of this is  $1 \pm 0.793$ , and where 30 units were used  $1 \pm 0.534$ .

The coefficients of dispersion were worked out for Collembola from six different soil types, and in almost all cases they were found to be greater than unity for separate species. Table 2 shows the average coefficients of dispersion over the whole sampling period. For total Collembola the coefficient of dispersion was greater than unity in all cases.

Table 2 Average Coefficients of Dispersion for species of Collembola on the different sampling sites

	<i>Onychiurus</i> <i>procamptus</i> <i>tricamptus</i>	<i>Friesia</i> <i>mirabilis</i>	<i>Tullbergia</i> <i>kraushaueri</i>	<i>Folsomia</i> <i>manolachei</i>	<i>Isotoma</i> <i>sensibilis</i>	<i>Isotomiella</i> <i>minor</i>	<i>Folsomia</i> <i>brevicauda</i>	<i>Tetracanthella</i> <i>wahlbergi</i>	<i>Anurida</i> <i>pygmaea</i>	<i>Symphyla</i> <i>pleona</i>	Total Collembola
Limestone grass- land (Feb. 1960— Dec. 1961) 24 samples	3.46	2.77	10.07	10.20	2.93	2.90	—	—	—	3.16	11.20
Alluvial grassland (April 1960— May 1961) 13 samples	5.53	2.68	9.98	7.77	2.67	3.53	—	—	—	2.23	13.01
Heather litter (Jan.—Dec. 1961) 13 samples	—	2.87	—	—	5.63	—	20.52	—	—	—	17.62
Hagg lip *) (May 1960— Dec. 1961) 5 samples	—	4.57	—	—	14.86	—	18.48	19.90	—	—	29.73
Hummock top *) (May 1960— Dec. 1961) 5 samples	—	1.42	—	—	8.27	—	17.91	—	8.64	—	21.94
<i>Juncus squarrosus</i> grassland (March 1960— Dec. 1961) 6 samples	—	4.77	—	—	2.53	—	—	—	—	—	7.99

\*) Note: These terms refer to two areas on the erosion complex (see HALE 1963).

From these data it can be seen that the distribution does not follow a Poisson expectation, and that there is a marked aggregation or under-dispersion of both individual species and total Collembola. HAARLØV (1960), using the same sample unit size as in this work, obtained much smaller values for the coefficient of dispersion of individual species of

Collembola; however, this author rightly points out that due to the scarcity of data (too few samples were taken) the conclusion that there is a random dispersion must be viewed with caution. POOLE (1961) obtained values of the coefficient of dispersion (termed by this author "relative variance") similar to those in the present work.

#### 4.1.3.2. The frequency distribution

The study of the frequency distribution of the sample unit values has been approached from two slightly different points of view, due to the types of data available:

i. For the sample unit values of total Collembola on a given soil type, comparison is made with the normal distribution curve; this is possible as no values of zero occur in the sample unit values. Here the sample unit values are grouped into frequency distributions round their individual means, with multiples of the standard deviations as the class boundaries. The mean value is taken as zero, sample unit values smaller than the mean being indicated by negative S. D. classes and sample units larger than the mean by positive S. D. classes. The data for the three main sampling sites (the average for the whole sampling period) are shown in Table 3. In all three cases there is a significant difference from the expected normal distribution.

Table 3 Frequency distribution of sample unit values about the mean (0) compared with expected values of a normal distribution

	Negative				Positive				$\chi^2$	d. f.	P
	2—3	1—2	0—1	0—1	1—2	2—3	3—4	4—5			
Standard Deviation classes											
Limestone grassland											
a. Observed	0	64	179	136	54	12	2	0	19.0	5	< 0.05
b. Expected	10	61	152	152	61	10					
Alluvial grassland											
a. Observed	0	26	110	54	22	12	1	0	42.2	5	< 0.001
b. Expected	5	31	77	77	31	5					
Heather litter											
a. Observed	0	10	110	41	22	7	3	0	55.6	3	< 0.001
b. Expected		31	66	66	31						

It can be seen that the distributions are skewed in all three cases, there being an excess of small negative deviates and large positive deviates. This is a typical frequency distribution where aggregations occur within a population (POOLE 1961), where most sample units are from areas of relatively low density but some sample units are from areas of high density. O'CONNOR (1957), PEACHEY (1959) and BANAGE (1960) have found similar skewed distributions in enchytraeids and nematodes. The data presented here show the total Collembola to be aggregated in the three soil types considered.

ii. For sample unit values of individual species, where a number of sample units contained no individuals, comparison of the distribution was made with a Poisson frequency. In all cases examined the distribution of individual species was found not to follow a Poisson distribution. An excess of both low and high values was found, as compared with the Poisson expectation. This indicates aggregation of individuals as in the case of the distribution of total Collembola.



#### 4.1.4. The statistical treatment of the data

Since the raw data obtained in the present work show that the sample unit values do not follow a normal distribution, a transformation of the data is indicated before using normal distribution statistics. QUENOUILLE (1950) has shown that when the variance (or standard deviation) increases with the mean, a logarithmic transformation is the most suitable. Fig. 1 shows an increase in the standard deviation with the mean for the data concerning total Collembola on Limestone grassland. In Figs. 5—7 a logarithmic transformation is made in the consideration of seasonal fluctuations in numbers.

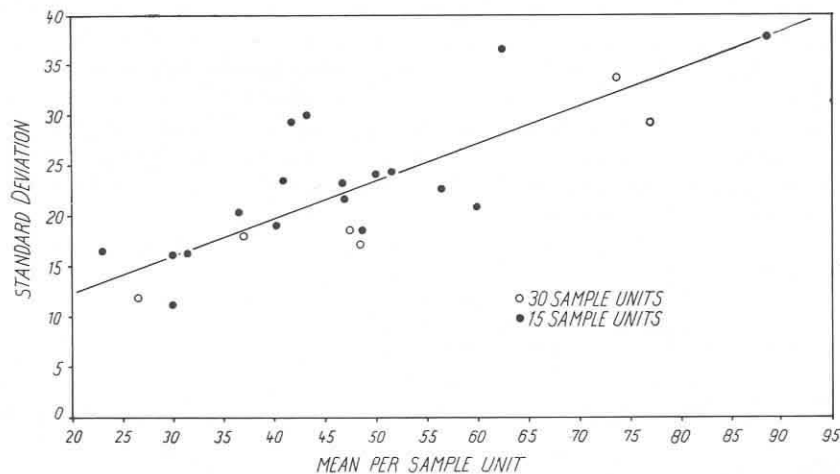


Fig. 1. Graph showing the relationship between the mean and the standard deviation in samples from Limestone grassland collected during 1960 and 1961. The line was fitted by eye.

#### 4.1.5. The biological significance of aggregation

COLE (1946) has advanced the hypothesis that whilst individual organisms occur clumped, i. e. in aggregations, "... each group may be relatively or entirely independent of all similar groups and, therefore, (the groups are) ... randomly distributed". In the case of a mixed population consisting of several species in which the individual species are known to be aggregated, random distribution of all the individuals in the population would be expected if the above statement were true. That is to say that aggregations of any one species would be distributed at random with respect to an aggregation of any other species. The coefficient of dispersion and the distribution of the sample unit values with respect to a normal distribution show marked aggregation for total Collembola, which suggests aggregation of more than one species at a given centre. POOLE (1961) points out that if this were not so, the different species aggregations would tend to balance one another out, and thus result in a total distribution that was almost random. Thus, it can be concluded that different species of Collembola tend to aggregate about the same centre of aggregation.

Two possibilities are evident to explain the formation of aggregations in soil microarthropods; firstly, aggregations may result from the slow dispersion of individuals from an egg batch, and, secondly, aggregations may result from the coming together of individuals at either a food source or as a result of being actively gregarious.

Evidence for the complementary distribution of species is provided by plotting the numbers of two different species in individual sample units against each other. In Fig. 2



this is done for the two species occurring commonly on the hagg lip zone, where species other than *Tetracanthella wahlgreni* and *Folsomia brevicauda* are uncommon. There is clearly a marked tendency for high numbers of each species to occur together.

The coefficient of dispersion varies with the degree of aggregation, and thus a high coefficient indicates a greater amount of aggregation than a low one. If aggregation results from egg batches, it would be expected that the degree of aggregation in a given species would be at its greatest at the time of egg hatching, and that some dispersal would occur afterwards, so reducing the amount of aggregation and the coefficient of dispersion. Information of the laying and hatching times of some species in the field at Moor House (HALE 1965a) and the monthly variations in the coefficients of dispersion were examined in the light of these data. No correlation was found between times of hatching and times of maximum aggregation in any species. Thus it seems unlikely that aggregations found during the course of this work resulted from egg batches.

POOLE (1961) has attempted to show that aggregations of Collembola are not related to egg clusters. This was done by comparing the egg batch size of three species with their coefficients of dispersion when an inverse relationship was shown. However, comparison with the data obtained during the present work (Table 4) shows no clear correlation so that in this respect it is concluded that there is no evidence to suggest that aggregations do not result from egg batches. The probability is that most aggregations are the result of individuals collecting together at some point after hatching. This certainly appears to be the case where swarming on snow and water surfaces has been recorded (DAVIES 1932; PACLT 1956).

Whilst the available data cast little light on the formation of aggregations they at least demonstrate their existence, and thus support the findings of earlier workers. The fact that aggregations either overlap, or contain more than one species, suggests the coming together of individuals at a food source, or similar microhabitat in which optimum conditions prevail. However, no support can be given to the contention of HAARLØV

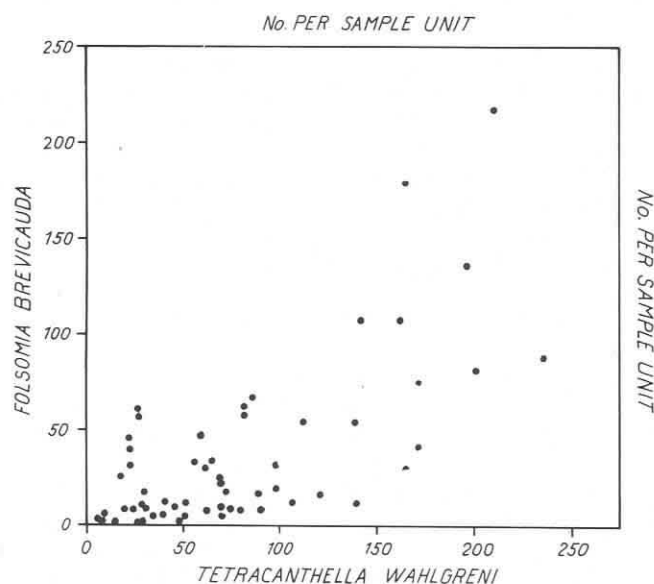


Fig. 2. The relationship between the numbers of *Tetracanthella wahlgreni* and *Folsomia brevicauda* occurring in the same sample units from the hagg lip zone.

Table 4 Comparison of egg batch sizes and coefficients of dispersion

Species	Mean Egg batch size & S. E. of mean	Coefficient of Dispersion	Authority
<i>Tullbergia krausbaueri</i>	1—2 5.5 $\pm$ 0.3	20.70—41.50 2.21—29.66	POOLE (1961) HALE
<i>Onychiurus procampatus</i>	4.7 $\pm$ 0.2	0.81—12.48	HALE
<i>Isotoma sensibilis</i>	20.0 $\pm$ 8.0	0.97—31.64	HALE
<i>Isotoma notabilis</i>	6—10	21.50—38.20	POOLE (1961)
<i>Isotomurus plumosus</i>	30—50	8.00— 8.60	POOLE (1961)

(1960) that the better the locomotory organs are developed the less aggregated is the distribution of the species in question. The average coefficients of dispersion for *Folsomia manolachei* (10.20) and *Isotoma sensibilis* (2.93), which are very active species, do not suggest a lesser degree of aggregation than is found in any of the species with poorly developed locomotory organs e. g. *Onychiurus procampatus* (3.46) and *Tullbergia krausbaueri* (10.07).

## 4.2. Vertical distribution

### 4.2.1. Distribution in 0—3 cm and 3—6 cm layers

GLASGOW (1939), AGRELL (1941), GISIN (1943), NIELSEN (1949), SCHALLER (1949), VAN DER DRIFT (1951), MURPHY (1953), BELLINGER (1954), KÜHNELT (1955) and POOLE (1961) have shown that micro-arthropods occur more commonly in the upper layers of the soil. MACFADYEN (1957) commented upon the fact that life tends to be concentrated at the meeting of two phases due to the photosynthetic demands of the plants which form the primary food source. SCHIMITSCHEK (1938), STÖCKLI (1946), WEIS-FOGH (1948), KÜHNELT (1950), MACFADYEN (1952), ELTON and MILLER (1954), HAARLØV (1955, 1960), MURPHY (1955), and KLIMA (1956) have shown that micro-arthropods occur where the pore spaces are largest, and according to HAARLØV (1955) the cavity size of the pore spaces decreases with depth in mineral soils. Thus, here again high densities are shown to occur in the upper soil layers.

During the course of this work it was found that on peat soils Collembola did not usually occur at a depth greater than 3 cm, i. e. they did not occur below the decomposition layer, in the peat proper. This was mainly due to waterlogging, and apparently below this depth pore spaces containing air are rare or absent; this was demonstrated by squeezing peat from the 3—6 cm layer under water, when few or no air bubbles appeared. Samples were taken on one occasion only from the 3—6 cm layer on the Heather litter site, on the *Juncus squarrosus* site and on bare peat; Collembola were absent. On the two mineral soils sample cores were taken regularly to a depth of 6 cm, and divided into two layers each 3 cm deep. In both these soils separation at this level divided the core into an upper layer containing the vegetation and the decomposition layer, and a lower layer consisting entirely of mineral matter permeated by plant roots.

All the data in this section are from 6 cm cores, divided into 3 cm layers, which were collected from two types of mineral soil on Limestone grassland and Alluvial grassland. In these samples it was possible to determine the extent to which different species penetrated into the soil, by counting the numbers in each of the two layers. The data resulting from such counts are shown in Table 5, and the figures listed are for total numbers over a period of one year. Only the more abundant species are shown.

Table 5 Depth distribution of Collembola on mineral soils

	Limestone grassland 1960		1961		Alluvial grassland 1960—1961	
	Nos. in 0—3 cm 3—6 cm	% in lower 3 cm	Nos in 0—3 cm 3—6 cm	% in lower 3 cm	Nos. in 0—3 cm 3—6 cm	% in lower 3 cm
<i>Friesea</i>	1361	22.3	896	25.6	753	15.9
<i>mirabilis</i>	391		308		142	
<i>Anurida</i>	32	61.0	77	54.7	41	55.0
<i>pygmaea</i>	50		93	—	50	
<i>Onychiurus</i>	328	17.6	410	9.5	436 80	15.5
<i>procampatus</i>	70		43			
<i>Onychiurus</i>	213	40.3	405	33.9		
<i>tricampatus</i>	144		208			
<i>Tullbergia</i>	1059	54.2	484	62.7	2482	42.9
<i>krausbaueri</i>	1382		812		1861	
<i>Tullbergia</i>	—	—	—	—	5	86.8
<i>denisi</i>					33	
<i>Folsomia</i>	4117	6.8	2121	9.9	1378	3.7
<i>manolachei</i>	299		232		53	
<i>Folsomia</i>	261	12.1	150	7.4	11	0.0
<i>4-oculata</i>	36		12		0	
<i>Folsomia</i> cf.	115	47.3	20	73.3	21	40.0
<i>brevifurca</i>	103		55		14	
<i>Isotoma</i>	538	2.7	411	5.3	572	1.6
<i>sensibilis</i>	13		23		9	
<i>Isotoma</i>	236	5.6	92	4.2	238	4.0
<i>viridis</i>	14		4		10	
<i>Isotoma</i>	324	2.4	108	6.9	238	0.4
<i>notabilis</i>	8		8		1	
<i>Isotomiella</i>	395	60.1	100	73.4	232	50.3
<i>minor</i>	595		276		235	
<i>Symphyleona</i>	422	1.6	719	1.9	196	2.0
	7		14		4	
Total	9890	26.7	6048	25.3	7301	25.7
Collembola	3604		2051		2572	

The highest total density of Collembola occurs in the upper 3 cm layer, and this agrees well with the results of other workers. Some species, namely *Anurida pygmaea*, *Tullbergia krausbaueri*, *Tullbergia denisi*, *Folsomia brevifurca* and *Isotomiella minor* have a higher density in the 3—6 cm layer, and these are the true soil forms. *Friesea mirabilis*, *Onychiurus procampatus* and *Onychiurus tricampatus* penetrate into the lower layer, but the majority of the Isotomidae and the Symphypleona are surface forms which only occasionally penetrate into the 3—6 cm layer, probably by entering earthworm burrows, or accidentally during sampling.

Sampling on the Limestone grassland site was carried out over a period of two years and in Table 6 comparison is made between the depth distribution of the species penetrating into the 3—6 cm layer in different years. Only those species whose density in the 3—6 cm layer exceeds 10% of the total are considered. With the exception of *Anurida pygmaea* there is a significant difference in the depth distribution in the two years considered for all species, and for the total numbers of Collembola. During 1961 *Friesea mirabilis*, *Tullbergia krausbaueri*, *Folsomia brevifurca* and *Isotomiella minor* occurred more commonly in the deeper level, whilst *Onychiurus procampatus* and *O. tricampatus* were

found significantly more frequently in the 0—3 cm layer. These differences in depth distribution may be associated with the reduction in population density in 1961, as compared with 1960 (a mean of 42,000/m<sup>2</sup> in 1961 and 53,000/m<sup>2</sup> in 1960). It is possible that this may be correlated with the increased spring (March—May) rainfall in 1961 (13 in) as compared with 1960 (9 in).

Table 6 Comparison of depth distribution in different years; Limestone grassland, 1960 and 1961

Species	1960		1961		$\chi^2$ for 1 degree of freedom	P
	Nos. in 0—3 cm layer	Nos. in 3—6 cm layer	Nos. in 0—3 cm layer	Nos. in 3—6 cm layer		
<i>Friesea mirabilis</i>	1361	391	896	308	4.21	< 0.05
<i>Anurida pygmaea</i>	32	50	77	93	0.89	> 0.05
<i>Onychiurus procampatus</i>	328	70	410	43	12.06	< 0.001
<i>Onychiurus tricampatus</i>	213	144	405	208	4.00	< 0.05
<i>Tullbergia krausbaueri</i>	1059	1382	484	812	12.73	< 0.001
<i>Folsomia</i> cf. <i>brevifurca</i>	115	103	20	55	15.28	< 0.001
<i>Isotomiella minor</i>	395	595	100	276	20.87	< 0.001
Total Collembola	9890	3604	6048	2051	5.02	< 0.05

Note: Comparison is made between the samples taken in two different years using the  $2 \times 2$  contingency table. Only those species occurring regularly in the 3—6 cm layer, i. e. where more than 10 % of the numbers occur below 3 cm, are considered.

The Alluvial grassland site was sampled monthly from May 1960 until May 1961, and in Table 7 comparison is made with samples collected from Limestone grassland over the same period. With the exception of *Anurida pygmaea* there is a significant difference between the two areas for all species concerned, and for total Collembola. This probably reflects to some extent the larger sizes of the pore spaces in the soil on the Limestone grassland, where, over the period concerned 28 % of the population occurred in the 3—6 cm layer as compared with 26 % on the Alluvial grassland.

#### 4.2.2. 'Lebensformen' and vertical distribution

GISIN (1943) constructed a classification of life forms in which the habitat in which the species lives is reflected to some extent in the modifications of the body form which the species possesses. An assessment of this classification is made here in the light of the information listed in Table 5, and the species are regrouped according to GISIN's classification of life forms in Table 8. The percentages occurring in the 3—6 cm layer on the Limestone grassland (1960 and 1961) and the Alluvial grassland are included, and it can be seen that there is a close correlation between the life forms and the vertical distribution. Those forms which possess well-developed eyes and pigment occur in the upper (0—3 cm) layer, and those species without pigment and eyes occur in the lower layer (3—6 cm).

Table 7 Comparison of depth distribution on Limestone grassland and Alluvial grassland, May 1960 to May 1961

Species	Limestone grassland		Alluvial grassland		$\chi^2$ for 1 degree of freedom	P
	Nos. in 0—3 cm layer	Nos. in 3—6 cm layer	Nos. in 0—3 cm layer	Nos. in 3—6 cm layer		
<i>Friesca mirabilis</i>	1241	409	753	142	27.23	< 0.001
<i>Anurida pygmaea</i>	39	73	41	50	2.20	> 0.05
<i>Onychiurus procampatus</i> and <i>tricampatus</i>	924	387	436	80	41.48	< 0.001
<i>Tullbergia krausbaueri</i>	1072	1455	2482	1861	139.54	< 0.001
<i>Folsomia</i> cf. <i>brevifurca</i>	34	89	21	14	12.57	< 0.001
<i>Isotomiella minor</i>	344	640	232	235	144.43	< 0.001
Total Collembola	10364	4087	7301	2572	14.68	< 0.001

Note: Comparison is made between samples taken on two different soil types during the same months, using a  $2 \times 2$  contingency table. Only those species occurring regularly in the 3—6 cm layer, i. e. where more than 10 % of the numbers occur below 3 cm, are considered.

Table 8 Correlation between GISIN's "Lebensformen" and vertical distribution

Lebensformen (Life form)	Species	% in lower layer (3—6 cm) of core		
		Limestone 1960	grassland 1961	Alluvial grassland
ATMOBIOS	<i>Isotoma viridis</i>	5.6	4.2	4.0
	<i>Symphyleona</i>	1.6	1.9	2.0
HEMIE-DAPHON				
a. Mesophil	<i>Friesca mirabilis</i>	22.3	25.6	15.9
	<i>Anurida pygmaea</i>	61.0	54.7	55.0
	<i>Folsomia manolachei</i>	6.8	9.9	3.7
	<i>Folsomia 4-oculata</i>	12.1	7.4	0.0
	<i>Isotoma notabilis</i>	2.4	6.9	0.4
b. Xerophil	<i>Isotoma sensibilis</i>	2.7	5.3	1.6
EUEDAPHON	<i>Onychiurus procampatus</i>	17.6	9.5	15.5
	<i>Onychiurus tricampatus</i>	40.3	33.9	
	<i>Tullbergia krausbaueri</i>	54.2	62.7	42.9
	<i>Tullbergia denisi</i>	—	—	86.8
	<i>Folsomia</i> cf. <i>brevifurca</i>	47.3	73.3	40.0
	<i>Isotomiella minor</i>	60.1	73.4	50.3

#### 4.2.3. Seasonal variation in vertical distribution

VOLZ (1934), AGRELL (1934), JACOT (1936, 1940), GLASGOW (1939), BAWEJA (1939), STRICKLAND (1947), BELFIELD (1956), SCHWEIZER (1956) and STÜCKLI (1957) have shown that changes in the vertical distribution of different species of mites and Collembola occur throughout the year. This is interpreted in most cases as a vertical migration

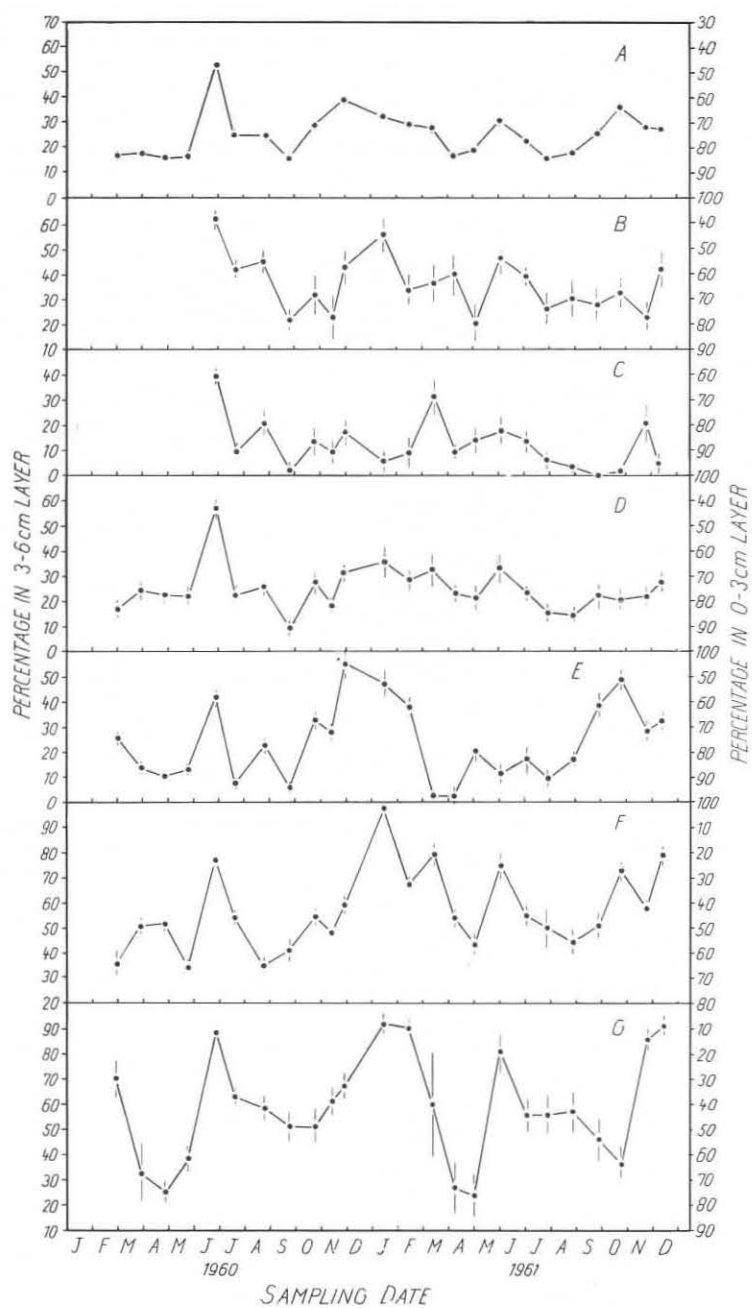


Fig. 3. Vertical distribution of Collembola on Limestone grassland during 1960 and 1961. A. Total Collembola; B. *Onychiurus tricampatus*; C. *Onychiurus procampatus*; D. *Onychiurus procampatus* and *Onychiurus tricampatus* combined; E. *Friesea mirabilis*; F. *Tullbergia krausbaueri*; G. *Isotomiella minor*.

during periods of adverse climatic conditions in the upper layers of the soil. However, FRENZEL (1936) and DHILLON and GIBSON (1962) found no evidence of seasonal changes in vertical distribution.

During the course of the present work, the fact that monthly samples were taken at two levels made possible an analysis of the data from the point of view of seasonal changes in vertical distribution. Only those species occurring commonly in both layers (0—3 cm and 3—6 cm) are considered, namely: *Friesea mirabilis*, *Onychiurus procampatus*, *Onychiurus tricampatus*, *Tullbergia krausbaueri* and *Isotomiella minor*. In Figs. 3 and 4 the numbers occurring in the 3—6 cm layer are plotted as a percentage of the total on each sampling date; the standard error of the mean is also indicated. On both the Limestone grassland (1960, 1961) and the Alluvial grassland, early summer and winter peaks occur, together with autumn and spring minima. There is thus a higher proportion of Collembola in the layer in early summer and winter, i. e. during periods of adverse weather conditions. In

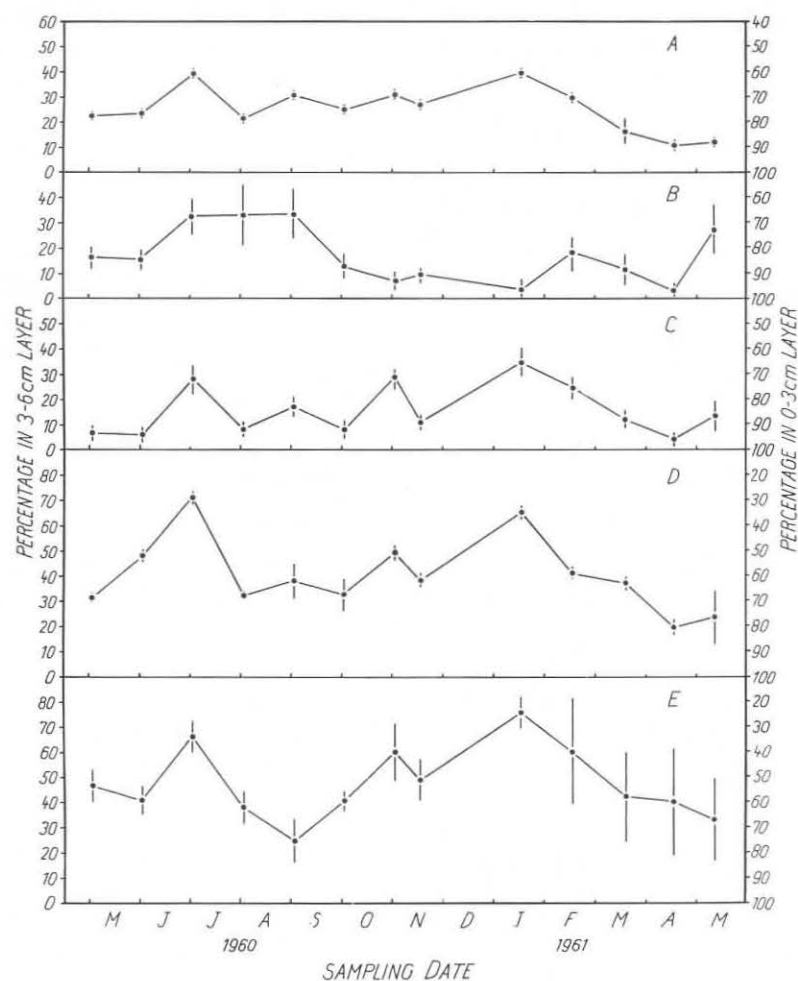


Fig. 4. Vertical distribution of Collembola on Alluvial grassland during 1960—1961. A Total Collembola; B. *Onychiurus procampatus* and *Onychiurus tricampatus*; C. *Friesea mirabilis*; D. *Tullbergia krausbaueri*; E. *Isotomiella minor*.



most cases the standard errors indicate a significant difference between the maxima and minima, and it can be concluded that seasonal changes in vertical distribution occur in both soil types studied. Early summer and winter maxima for Collembola in the lower layers of soil have been recorded by FORD (1937), GLASGOW (1939) and POOLE (1961); winter maxima only have been recorded by STRENZKE (1949) and MACFADYEN (1952) for both mites and Collembola.

Whilst the evidence strongly suggests a vertical migration in order to avoid adverse climatic conditions in the upper layers of the soil in summer and winter, it is possible that these data show a vertical differential mortality, or both this and vertical migration. The data available do not permit an analysis to show which of these phenomena occur.

#### 4.3. Seasonal variations in numbers

##### 4.3.1. Annual maxima and minima

On both Limestone grassland and Alluvial grassland the six commonest species of Collembola were selected for study, and on the Heather litter site the three commonest species; other species occurred in insufficient numbers for a worthwhile analysis. The

Table 9 Peak numbers of Collembola on three sampling sites at Moor House in 1960 and 1961; from three monthly running means

Species	Sam- pling Site	Year	Month											
			J	F	M	A	M	J	J	A	S	O	N	D
<i>Friesea mirabilis</i>	LG	1960	—	.	×	.	.	.	.	.	×	.	.	.
		1961	.	.	×	.	.	.	.	.	×	.	.	.
	AG	1960	—	—	—	—	.	.	.	.	×	.	.	.
<i>Onychiurus procampatus</i> and <i>tricampatus</i>	LG	1961	.	.	.	×	.	.	.	.	.	×	.	.
		1960	—	.	.	.	.	.	×	?	.	.	.	×
	AG	1961	×	?	.	×	?	.	.	.	×	.	.	×
<i>Tullbergia krausbaueri</i>	AG	1960	—	—	—	—	.	.	×	.	.	×	.	.
		1961	—	.	.	.	×	.	.	.	.	.	×	.
	LG	1961	.	.	×	.	.	.	.	.	.	×	.	.
<i>Folsomia manolachei</i>	AG	1960	—	—	—	—	.	.	.	.	×	.	.	.
		1961	.	.	.	.	.	×	.	.	.	.	×	.
	LG	1961	—	—	—	—	.	.	×	.	.	×	?	.
<i>Folsomia brevicauda</i>	HL	1961	.	.	.	×	.	.	.	.	.	.	×	.
<i>Isotoma sensibilibis</i>	LG	1960	—	.	.	.	×	.	.	.	.	.	.	.
		1961	.	.	×	?	.	.	.	×	.	.	.	.
	AG	1960	—	—	—	—	.	.	×	.	.	.	.	.
<i>Isotomiella minor</i>	LG	1961	.	.	.	.	.	×	.	.	.	.	.	.
		1960	—	.	.	.	.	.	×	.	.	.	×	.
	AG	1961	.	.	.	.	.	.	×	.	.	.	×	.
Symphypleona	LG	1960	—	—	—	—	.	.	.	.	×	.	.	.
		1961	.	×	.	.	.	.	×	.	×	?	.	.
	AG	1960	—	—	—	—	.	×	.	.	.	.	×	.
Total Collembola	LG	1960	—	.	.	.	×	.	.	.	.	×	.	.
		1961	.	.	×	.	.	.	.	.	.	.	×	.
	AG	1960	—	—	—	—	.	.	×	.	.	.	.	.
	HL	1961	.	.	.	.	.	×	.	.	.	.	.	.

Limestone grassland (LG), Alluvial grassland (AG), Heather litter (HL) no data (—).

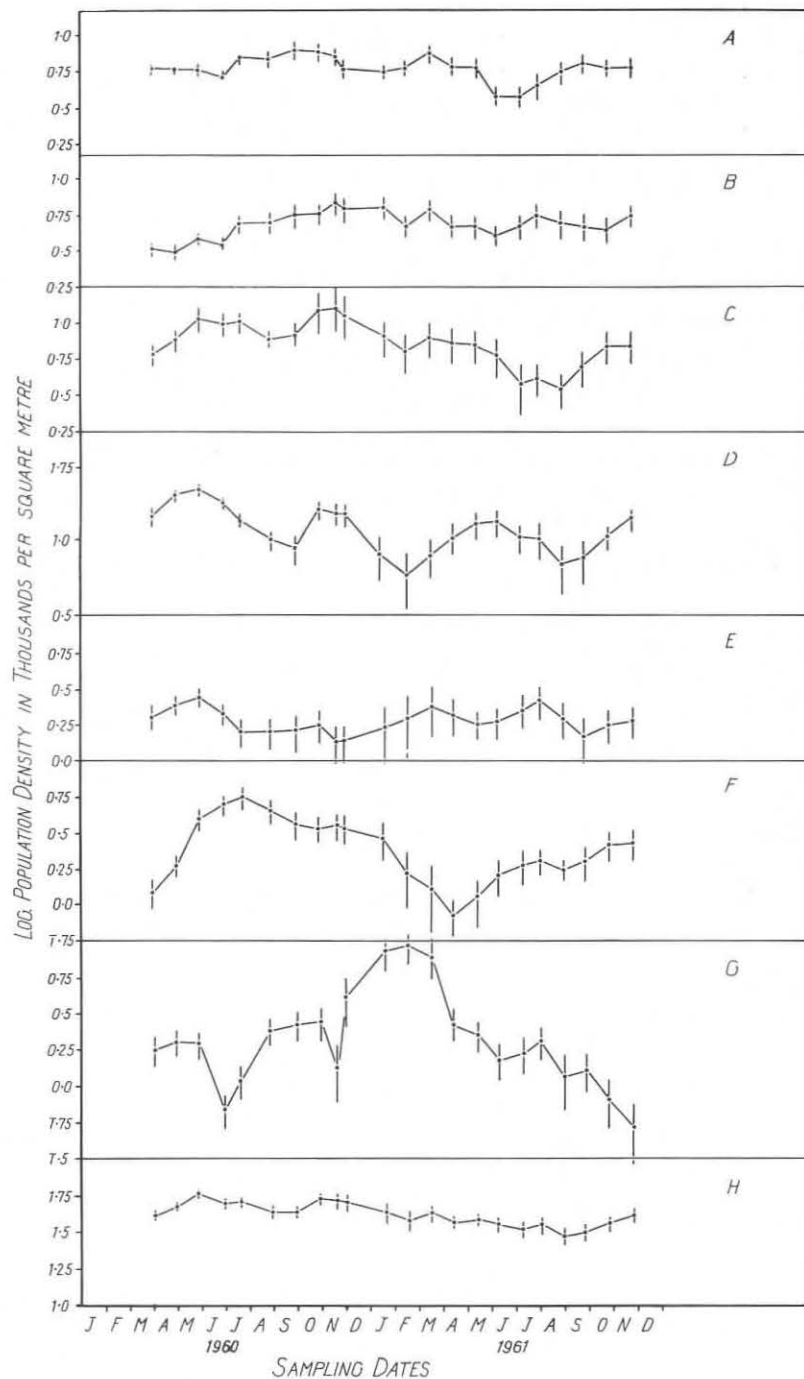


Fig. 5. Three monthly running means and standard errors of the means of the numbers of Collembola on Limestone grassland during 1960 and 1961. A. *Friesia mirabilis*; B. *Onychiurus procampatus* and *Onychiurus tricampatus*; C. *Tullbergia krausbaueri*; D. *Folsomia manolachei*; E. *Isotoma sensibilis*; F. *Isotomiella minor*; G. *Symphypleona*; H. Total Collembola.

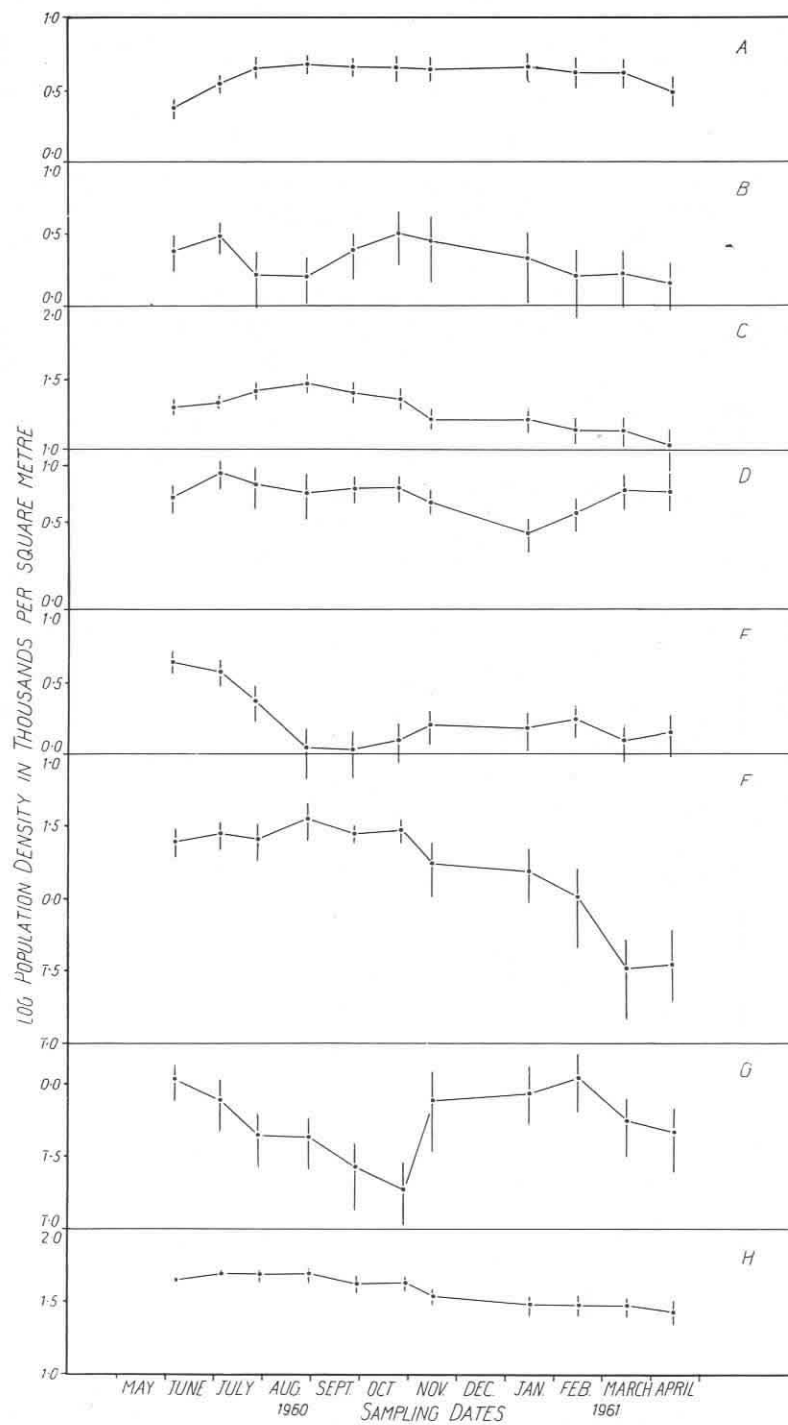


Fig. 6

Fig. 6. Three monthly running means and standard errors of the means of the numbers of Collembola on Alluvial grassland during 1960—1961. A. *Friesea mirabilis*; B. *Onychiurus procampatus* and *Onychiurus tricampatus*; C. *Tullbergia krausbaueri*; D. *Folsomia manolachei*; E. *Isotoma sensibilis*; F. *Isotomiella minor*; G. *Symphyleona*; H. Total Collembola.

data obtained from monthly samples were plotted logarithmically as three month running means, together with the standard error of the mean for each point (Figs. 5—7). No obvious pattern could be seen in the raw data, but consideration of the running means reveals what appears to be a general pattern. Early summer and winter peaks are apparent in the total numbers of Collembola on Limestone grassland in both 1960 and 1961, and early summer peaks are also present on Alluvial grassland in 1960 and Heather litter in 1961.

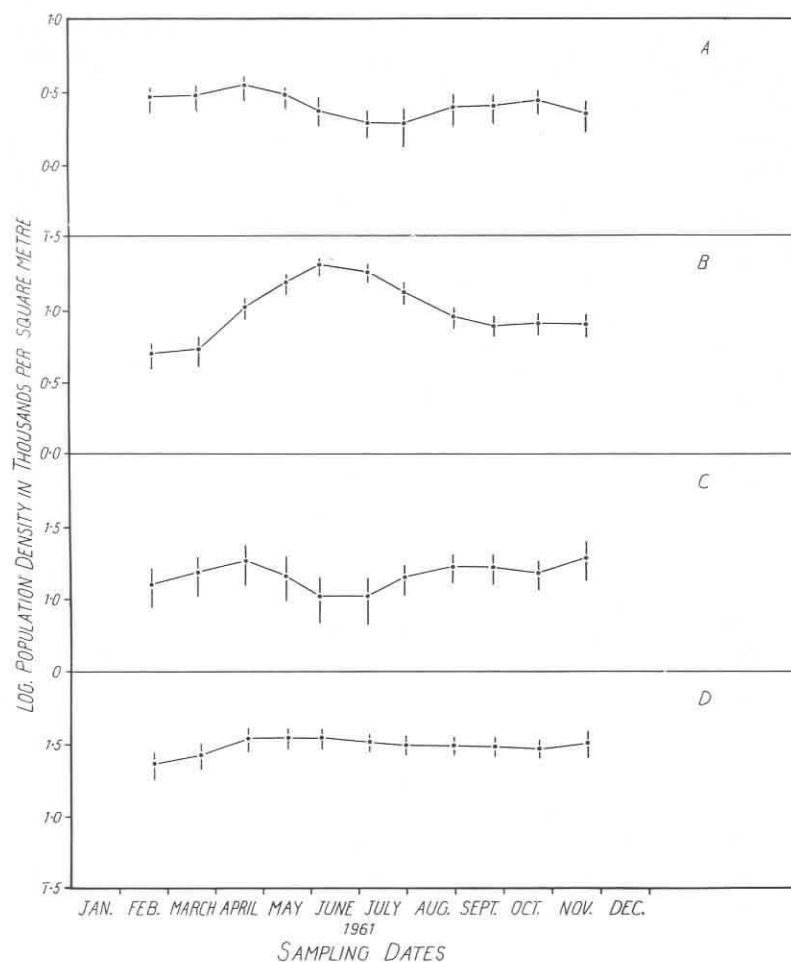


Fig. 7. Three monthly running means and standard errors of the means of the numbers of Collembola on Heather litter during 1961. A. *Friesea mirabilis*; B. *Isotoma sensibilis*; C. *Folsomia brevicauda*; D. Total Collembola.

It is thought that the saw-toothed effect of the graphs showing the raw data possibly results in part from different extraction efficiencies on different dates. The occurrence of peak populations of different species, derived from the running means, is shown in Table 9. Two groupings can be made concerning the seasonal fluctuations in numbers of these species:

- i. Species having a single annual peak in numbers e. g. *Isotoma sensibilis*.
- ii. Species having two annual peaks in numbers e. g. *Friesia mirabilis*, *Onychiurus* spp., *Tullbergia krausbaueri*, *Folsomia* spp., *Isotomiella minor*.

It would be expected that population peaks would occur shortly after the period of maximum oviposition, when temperatures are favourable to egg development. In the case of species in the first group e. g. *Isotoma sensibilis*, it has been shown that the period of maximum oviposition begins in April (HALE 1965a). Since these data are accurate to within  $\pm 1$  month (monthly collections were made) eggs could have been laid in the field in March. The population peak for 1960 occurs in May/June, and thus the correlation between egg laying and the population peak is a good one. At no other time were eggs laid, and first instar individuals were present in samples only about the time of the peak population density.

Of the species having two annual population peaks, two divisions can be made. Firstly, there are those species having spring and autumn peaks, i. e. *Friesia mirabilis* and *Folsomia* spp. No data concerning egg laying in these species are available, but first instar individuals occurred in the samples during spring and autumn, and the available information suggests two generations per year. Secondly, there are those species having summer and early winter peaks in numbers, i. e. *Onychiurus* spp., *Tullbergia krausbaueri* and *Isotomiella minor*. All these species are members of the euedaphon (forms living in the soil rather than on it), and in all species except *Isotomiella minor*, where no information is available, eggs were laid throughout the summer and early autumn (HALE 1965a). The peaks in numbers of these species are probably caused by the hatching of overwintering eggs in summer and by eggs laid during the summer in early winter. It is possible that in *Isotomiella minor* and *Onychiurus tricampatus* there may be two generations a year.

It can be seen by consideration of peaks occurring in the three monthly running averages of the data that there is a suggestion of an annual cycle which can be correlated with the periods of egg laying in the species where these data exist.

#### 4.3.2. Comparison with the results of previous workers

Direct comparison of the Moor House data with those of other workers is difficult because of the short breeding season experienced under sub-arctic conditions. Most other work has been carried out on low-lying meadow-land or woodland, where climatic conditions are less inclement. However, under arctic conditions, AGRELL (1941) and HAMMER (1944) found summer peaks, which agree with the results in the present paper. In contrast to this, most of the work in more temperate climates, and on lower ground, has shown autumn peaks with low numbers in summer.

GLASGOW (1939) records an April peak for total Onychiuridae and a significant minimum in January between peaks in December and February/March, for the three species *Onychiurus armatus* (TULLBERG 1869) not sensu GÄSIN 1952, *Tullbergia quadrispina* (BÖRNER 1901) and *Tullbergia krausbaueri*. Such a minimum also occurs in the raw data in the present work for totals of *Onychiurus* spp. on the Limestone grassland and in *Tullbergia krausbaueri*. In the case of *Onychiurus* spp. examination of the comparative numbers of different instars reveals that the February 1961 peak, following the January trough, is a result of an early hatch of overwintering eggs; a significantly higher percentage of first and second instars of *Onychiurus tricampatus* occurs in February ( $\chi^2 = 5.22$

for 1 degree of freedom;  $P < 0.025$ ). DHILLON and GIBSON (1962) have found April and December peaks in *Onychiurus armatus* (TULLBERG 1869) not sensu GISIN 1952, and POOLE (1961) found an August maximum for *Tullbergia krausbaueri*.

For *Isotoma* spp. both POOLE (1961) and DHILLON and GIBSON (1962) have found August peaks, but BELLINGER (1954) found a May peak in *Isotoma eunotabilis* FOLSOM 1937 which agrees with the data presented here for *Isotoma sensibilis*; in other areas the same author found later peaks in the same species. DHILLON and GIBSON (1962) found an August peak in *Friesia mirabilis* which corresponds to that shown by the present data. BELLINGER (1954) records April and August peaks in *Sminthurus fitchi* FOLSOM 1896, and DHILLON and GIBSON (1962) found March, July and September peaks in total Symphypleona; spring and autumn peaks were recorded at Moor House in this group and possibly a summer peak also occurred.

The data provided here concerning seasonal variations in numbers generally support the views expressed as a result of the examination of the biological data (HALE 1965a); that is to say:

i. Members of the Isotomidae, with the possible exception of *Isotomiella minor*, probably have only one generation a year under the climatic conditions prevailing at Moor House.

ii. *Friesia mirabilis*, *Onychiurus tricampatus*, *Tullbergia krausbaueri*, *Folsomia* spp. and the Symphypleona may have two generations, but probably not more, under Moor House conditions.

#### 4.4. The fauna of different sampling areas

##### 4.4.1. Treatment of the data

In the present work the differences between the various sampling areas, with respect to total numbers, the numbers of various species and the species 'spectrum', are considered from the statistical point of view. This method of approach is used in preference to the sociological methods of continental workers, e. g. AGRELL (1941), HAARLØV (1960), CASSAGNAU (1961), in that it is not affinities between different species of Collembola, but differences in the faunas of various habitats that it is desired to establish. GISIN (1943) has used a scale of abundance to indicate the numbers of Collembola in different samples; in this work the raw data are used for comparative purposes. In order to allow for seasonal fluctuations in numbers, the data for a period of twelve months have been pooled. In the case of the Limestone grassland, Heather litter and *Juncus squarrosus* grassland areas, the data compared are for the same months, and in most cases for the same dates; this is also the case for the Limestone grassland and Alluvial grassland areas. However, the sampling of Alluvial grassland overlapped that of Heather litter and *Juncus squarrosus* grassland by only five months.

In this section means per sample unit refer to the sample unit size of 11.35 cm<sup>2</sup>, and are not corrected for an area of 10 cm<sup>2</sup>; this was unnecessary for comparative purposes.

##### 4.4.2. Qualitative differences

Table 10 shows that six species, namely *Friesia mirabilis*, *Onychiurus* spp., *Tullbergia krausbaueri*, *Folsomia manolachei*, *Isotoma sensibilis* and *Isotomiella minor* dominated the fauna of the four main sampling sites. All these species were present in large numbers on the Limestone grassland and Alluvial grassland; in the Heather litter members of Gisin's (1943) "Euedaphon", namely *Onychiurus procampatus*, *Onychiurus tricampatus*, *Tullbergia krausbaueri*, and *Isotomiella minor* were either absent or present in very small numbers, and *Folsomia manolachei* was replaced by *Folsomia brevicauda*. On the *Juncus squarrosus* grassland the numbers of *Folsomia brevicauda* were greatly reduced, but members of the Symphypleona occurred more commonly.

Whilst obvious differences occur between the *Juncus squarrosus* grassland, the Heather litter, and the two grassland areas, differences between these last two are less obvious. LOUSLEY (1950) has pointed out that plant rarities within a habitat are frequently better indicators of variations between habitats than are the commoner species, and this clearly also applies in the case of the Collembola of these two areas. Table 10 shows that *Hypogastrura denticulata*, *Tullbergia denisi*, *Folsomia litsteri*, *Entomobrya nicoleti* and *Lepidocyrtus lignorum* occurred more frequently on the Alluvial grassland than on the Limestone grassland, whereas *Folsomia quadrioculata* was commoner on the latter area. Two other species which occurred on the Limestone grassland, and were apparently absent from the Alluvial grassland, were *Tullbergia affinis* and *Tetracanthella wahlgreni*; the former was obtained frequently in crumbled samples from Limestone grassland extracted using a Tullgren funnel, but was absent in similar samples from other areas. *Tetracanthella wahlgreni* occurred in very small numbers in the *Cladonia rangiferina* on the

Table 10 Total numbers of Collembola collected in quantitative samples taken on the four main sampling sites in twelve months

Species	Limestone grassland 195 units	Alluvial grassland 195 units	Heather litter 195 units	<i>Juncus</i> grassland 57 units
<i>Hypogastrura scotica</i>	0	0	1	0
<i>Hypogas trura denticulata</i>	7	158	0	1
<i>Willemia anophthalma</i>	2	0	8	0
<i>Friesea mirabilis</i>	1204	857	567	232
<i>Brachystomella parvula</i>	1	0	0	0
<i>Anurida pygmaea</i>	170	84	109	0
<i>Anurida forsslundi</i>	0	0	1	0
<i>Anurida granaria</i>	0	1	0	0
<i>Neanura muscorum</i>	0	0	25	0
<i>Onychiurus absoloni</i>	1	0	0	0
<i>Onychiurus procampatus</i>	1083	443	0	1
& <i>tricampatus</i>				
<i>Onychiurus latus</i>	0	0	52	7
<i>Tullbergia krausbaueri</i>	1296	4154	8	0
<i>Tullbergia affinis</i>	1	0	0	0
<i>Tullbergia denisi</i>	3	38	0	0
<i>Tetracanthella wahlgreni</i>	1	1	160	0
<i>Tetracanthella brachyura</i>	0	0	0	3
<i>Folsomia brevicauda</i>	0	0	3361	11
<i>Folsomia 4-oculata</i>	162	7	1	0
<i>Folsomia manolachei</i>	2285	1281	0	0
<i>Folsomia cf. brevifurca</i>	75	35	0	0
<i>Folsomia litsteri</i>	4	31	0	0
<i>Isotomiella minor</i>	376	419	0	0
<i>Isotoma sensibilis</i>	432	488	2254	231
<i>Isotoma notabilis</i>	116	193	7	1
<i>Isotoma viridis</i>	95	185	22	12
<i>Isotoma antennalis</i>	0	0	0	1
<i>Isotoma olivacea</i>	44	82	0	3
<i>Isotoma infusata</i>	1	0	0	0
<i>Isotomurus palustris</i>	0	1	1	17
<i>Entomobrya nicoleti</i>	1	12	1	0
<i>Entomobrya multifasciata</i>	1	1	0	0
<i>Willowsia buski</i>	0	0	13	0
<i>Lepidocyrtus cyaneus</i>	0	0	0	2
<i>Lepidocyrtus lignorum</i>	1	10	32	0
<i>Pseudosinella alba</i>	2	0	0	0
<i>Tomocerus minor</i>	0	0	8	0



Limestone grassland, but both the lichen and this species of Collembola were absent from the Alluvial grassland.

Species characteristic of the Heather litter are *Neanura muscorum*, *Onychiurus latus*, *Tetracanthella wahlgreni* which is associated with the lichens epiphytic on the *Calluna* stems, *Folsomia brevicauda*, *Willowsia buski* and *Tomocerus minor*. On the moor-edge zones of *Juncus squarrosus*, three species distinguish the fauna from those of the other three main sampling sites; *Isotoma antennalis*, *Isotomurus palustris* and *Lepidocyrtus cyaneus* were virtually absent elsewhere on the main sampling sites, but occurred commonly in qualitative samples from *Juncus squarrosus* grassland.

Whilst this work is largely devoted to the Arthropleona, identification of the Symphypleona has shown that several species appear to be characteristic of certain soil types. Thus, *Sminthurides pumilis* (KRAUSBAUER 1898), *Sminthurinus elegans* (FITCH 1863), *Sminthurinus aureus* (LUBBOCK 1862), *Sminthurinus niger* (LUBBOCK 1867), and *Bourletiella viridescens* STACH 1920 sensu GISIN 1948 have been recorded only from mineral soils, *Sminthurides malmgreni* (TULLBERG 1876), *Sminthurides parvulus* (KRAUSBAUER 1898), *Arrhopalites principalis* STACH 1945, *Dicyrtoma minuta* (O. FABRICIUS 1873) and *Dicyrtoma fusca* (LUCAS 1842) from peat soils and *Sminthurides signatus* (KRAUSBAUER 1898) and *Bourletiella hortensis* (FITCH 1863) from areas of peat erosion.

#### 4.4.3. Quantitative differences

Limestone grassland supports a higher density of Collembola than any of the other main sampling areas; Alluvial grassland, Heather litter and *Juncus squarrosus* grassland support progressively lower densities, the last area having a density of less than half that of the Limestone grassland; this is shown in Table 11. This is in direct contrast to what has been shown for other groups of soil animals (CRAGG 1961), where high densities have

Table 11 Comparison of the mean annual numbers of the commoner species of Collembola on the four main sampling sites, per sample unit 11.35 cm<sup>2</sup>; the standard error of the mean is also shown

Species									
Sampling site	<i>Friesia mirabilis</i>	<i>Onychiurus</i> spp.	<i>Tullbergia krausbauei</i>	<i>Folsomia manolachei</i>	<i>Folsomia brevicauda</i>	<i>Isotoma sensibilis</i>	<i>Isotomiella minor</i>	Symphy-pleona	Total Collembola
Limestone grassland 1960 (units 6 cm deep)	6.87 ± 0.26	4.89 ± 0.23	9.99 ± 0.64	17.31 ± 0.81	0	2.16 ± 0.12	3.88 ± 0.23	1.68 ± 0.14	52.92 ± 1.35
Limestone grassland May 1960 to May 1961. cf. Alluvial grassland. (units 6 cm deep)	6.93 ± 0.27	5.54 ± 0.26	10.65 ± 0.70	15.41 ± 0.78	0	2.14 ± 0.12	4.15 ± 0.26	3.41 ± 0.22	52.86 ± 1.31
Alluvial grassland May 1960 to May 1961 (units 6 cm deep)	3.98 ± 0.24	2.24 ± 0.25	19.30 ± 1.20	5.81 ± 0.56	0	2.58 ± 0.22	2.08 ± 0.24	0.89 ± 0.12	43.69 ± 1.64
Heather litter 1961 (units 3 cm deep)	2.94 ± 0.21	0	.	0	17.41 ± 1.51	11.68 ± 0.78	0	0.87 ± 0.12	35.17 ± 1.90
<i>Juncus squarrosus</i> grassland 1961 (units 3 cm deep)	4.07 ± 0.63	.	0	0	.	4.07 ± 0.37	0	11.74 ± 2.52	20.93 ± 2.86

Note: Less than 0.2 per sample unit (.).

Table 12 Differences between Means and Standard Errors of the Difference for samples of Collembola on the various sampling sites

AG HL Jsqr			AG HL Jsqr		
2.95 ± 0.41 P = < 0.001	3.23 ± 0.38 P = < 0.001	2.10 ± 0.71 P = < 0.010	LG	3.30 ± 0.41 P = < 0.001	5.55 ± 0.32 P = < 0.001
	1.40 ± 0.32 P ± < 0.010	0.09 ± 0.68 P = < 0.900			2.24 ± 0.26 P = < 0.001
		1.13 ± 0.67 P = < 0.010			—
A. <i>Friesea mirabilis</i>			B. <i>Onychiurus</i> spp.		
AG HL Jsqr			AG HL Jsqr		
8.65 ± 1.47 P = < 0.001	6.13 ± 0.62 P = < 0.001	6.13 ± 0.62 P = < 0.001	LG	9.60 ± 1.05 P = < 0.001	12.08 ± 0.91 P = < 0.001
	19.30 ± 1.20 P = < 0.001	19.30 ± 1.20 P = < 0.001			5.81 ± 0.60 P = < 0.001
		—			—
C. <i>Tullbergia krausbaueri</i>			D. <i>Folsomia manolachei</i>		
AG HL Jsqr			AG HL Jsqr		
0.44 ± 0.28 P = < 0.20	9.46 ± 0.81 P = < 0.001	1.83 ± 0.42 P = < 0.001	LG	2.07 ± 0.39 P = < 0.001	1.93 ± 0.20 P = < 0.001
	9.10 ± 0.81 P = < 0.001	1.47 ± 0.43 P = < 0.001			2.08 ± 0.24 P = < 0.001
		7.63 ± 0.86 P = < 0.001			—
E. <i>Isotoma sensibilis</i>			F. <i>Isotomiella minor</i>		

AG	HL	Jsq		AG	HL	Jsq	
2.52 ± 0.46 P = < 0.001	2.89 ± 0.54 P = < 0.001	7.98 ± 2.58 P = < 0.001	LG	9.17 ± 2.52 P = < 0.001	6.36 ± 2.63 P = < 0.020	20.60 ± 3.38 P = < 0.001	LG
	0.02 ± 0.16 P = < 0.900	10.85 ± 2.53 P = < 0.001	AG		8.52 ± 2.51 P = < 0.001	22.76 ± 3.29 P = < 0.001	AG
		10.87 ± 2.53 P = < 0.001	HL			14.24 ± 3.43 P = < 0.001	HL
G. Total Symphypleona				H. Total Collembola			

Note. In the Table the differences between the means are shown together with the Standard Error of the Difference and the Probability (P) of the data being similar.

AG — Alluvial Grassland. LG — Limestone Grassland. Jsq — *Juncus squarrosus* grassland. HL — Heather litter

been recorded from *Juncus squarrosus* areas. The highest density recorded on Limestone grassland was on 14 November 1960, when an average density of  $77,950 \pm 8,600$  individuals per m<sup>2</sup> was estimated. Maxima for the other sampling areas are as follows:

Alluvial grassland	(26. 9. 60)	$55,860 \pm 7,330$ per m <sup>2</sup>
Heather litter	(11. 12. 61)	$42,350 \pm 10,250$ per m <sup>2</sup>
<i>Juncus squarrosus</i>	(20. 2. 61)	$38,890 \pm 6,870$ per m <sup>2</sup>

When, however, the microdistribution of Collembola is considered, the specialised fauna associated with the hagg lip (HALE 1963) gives the highest densities yet recorded; on 4 December 1961,  $230,000 \pm 28,400$  individuals per m<sup>2</sup> were estimated, over 50 % of which were *Tetracanthella wahlgreni*.

Consideration of the dominant species shows that:

1. *Friesia mirabilis* has a significantly different density on all areas, with the exception of the Alluvial grassland and the *Juncus squarrosus* areas (Tables 11 and 12).
2. *Onychiurus* spp. have a significantly greater density on Limestone grassland than on Alluvial grassland, the species being virtually absent on the other sampling sites.
3. *Tullbergia krausbaueri* is significantly commoner on the Alluvial grassland than on the Limestone grassland, in contrast to the last species, but again is virtually absent on the other sampling sites.
4. *Folsomia manolachei* has a distribution similar to *Onychiurus* spp. and is replaced on the peat soils by *Folsomia brevicauda*.
5. *Isotoma sensibilis* is ubiquitous, the highest densities occurring on the Heather litter site; the density on *Juncus squarrosus* is significantly higher than those on the Alluvial and Limestone grasslands where there is no significant difference (Table 12 E).
6. *Isotomiella minor* has a distribution similar to *Onychiurus* spp. and *Folsomia manolachei*; the greatest densities occur on Limestone grassland.
7. Symphypleona have significantly higher densities on *Juncus squarrosus* than elsewhere.

The data concerning relative population densities of these species is summarised in Tables 11 and 12.

#### 4.4.4. Annual differences within a single vegetation type

The Limestone grassland is the only area for which there is more than one year's data. In Table 13 comparisons are made between the numbers of the commoner species in 1960 and 1961. In *Friesea mirabilis*, *Onychiurus* spp., and *Isotoma sensibilis* there is no significant difference between the average densities in different years. In *Tullbergia krausbaueri*, *Folsomia manolachei* and *Isotomiella minor* there is a significant decrease in numbers in 1961 as compared with 1960, whereas an increase occurs in the *Symphyleona* in 1961. The overall picture is of a reduction in the average density in 1961 as compared with 1960.

Table 13 Comparison of numbers and species of Collembola in different years on Limestone grassland, 1960 and 1961. The figures are means per sample unit 11.35 cm<sup>2</sup> and 6 cm deep

Species	<i>Onychiurus</i> spp.	<i>Friesea mirabilis</i>	<i>Tullbergia krausbaueri</i>	<i>Isotoma sensibilis</i>	<i>Isotomiella minor</i>	<i>Folsomia manolachei</i>	<i>Symphyleona</i>	Total Collembola
Means per sample unit 1960 (A)	4.89	6.87	9.99	2.16	3.88	17.31	1.68	52.92
Means per sample unit 1961 (B)	5.55	6.17	6.13	2.22	1.93	12.08	3.76	41.53
Difference (A — B)	+ 0.67	— 0.70	— 3.86	+ 0.06	— 1.95	— 5.23	+ 2.08	— 11.39
Standard Error of difference	0.43	0.45	1.01	0.26	0.35	1.37	0.60	2.60
P	> 0.05	> 0.05	< 0.001	> 0.05	< 0.001	< 0.001	< 0.001	0.001

#### 4.4.5. Microdistribution

Whilst on the Limestone grassland and the Alluvial grassland it is difficult to see any obvious differences in the plant cover, which could give rise to different microhabitats, on the other two areas differences could be seen. Thus, on the *Juncus squarrosus* site possible differences could occur within and between the rosettes of *Juncus squarrosus*. On the Heather litter site areas of *Sphagnum rubellum* could be differentiated clearly from patches of *Cladonia* spp.; in this latter case differences in the Collembola would be expected

Table 14. Comparison of the distribution of Collembola in and between the rosettes of *Juncus squarrosus*, 9. 5. 1960

Species	<i>Friesea mirabilis</i>	<i>Isotoma sensibilis</i>	Total Collembola
Mean per sample unit (11.35 cm <sup>2</sup> ) around rosettes	9.14	2.66	11.93
Mean per sample unit (11.35 cm <sup>2</sup> ) between rosettes	10.56	1.35	13.60
Difference between means and S. E. of difference	1.42 ± 2.17	1.31 ± 1.03	1.67 ± 2.71
P	> 0.05	> 0.05	> 0.05

due to the differences in water content between the wet, mossy areas, and the dry areas where lichens were abundant.

In order to ascertain whether or not there was a difference in the distribution of Collembola on the *Juncus squarrosus* site, in and between rosettes, 15 unit samples were taken from both areas on the same date; a summary of the data is given in Table 14. It can be seen from these results that no significant differences occurred in the distribution of Collembola with respect to rosettes on the *Juncus squarrosus* site.

To examine possible differences occurring in different vegetation types on the heather moor, an analysis was made for the two species *Folsomia brevicauda* and *Tetracanthella wahlgreni*; in the random samples collected from Heather litter, 101 samples contained *Sphagnum rubellum* and 21 units *Cladonia* spp. Table 15 summarises the data concerning the Collembola extracted from these samples. It can be seen that *Folsomia brevicauda* occurred in significantly higher densities in *Sphagnum* than in *Cladonia*, whereas the reverse is the case in *Tetracanthella wahlgreni*. This is also supported by data obtained from counts of Collembola from samples of 25 cm<sup>2</sup> surface area taken from sites where *Cladonia* and *Sphagnum* were actually in contact; a comparison of 20 such units, extracted in an ordinary Tullgren funnel, is made in Table 16. Again *Folsomia brevicauda* occurred in higher densities in *Sphagnum* and *Tetracanthella wahlgreni* in significantly higher densities in *Cladonia*. Thus differences occur within microhabitats on the heather moor comparable with those seen in the erosion complex (HALE 1963).

Table 15 Comparison of the density of two species of Collembola in different microhabitats on heather moor, from random samples. Sample units 11.35 cm<sup>2</sup> and 3 cm deep

Species	<i>Folsomia brevicauda</i>	<i>Tetracanthella wahlgreni</i>
Mean per sample unit in <i>Sphagnum rubellum</i>	19.31	0.42
Mean per sample unit in <i>Cladonia</i> spp.	10.95	5.05
Difference between means and S. E. of difference	8.36 ± 3.49	4.63 ± 1.65
P	< 0.02	< 0.01

Table 16 Comparison of the numbers of two species of Collembola from 25 cm<sup>2</sup> sample units of *Sphagnum* and *Cladonia* in contact

Species	<i>Folsomia brevicauda</i>	<i>Tetracanthella wahlgreni</i>
Mean per sample unit in <i>Sphagnum rubellum</i> (20 units)	21.50	1.15
Mean per sample unit in <i>Cladonia</i> spp. (20 units)	1.30	29.60
Difference between means and S. E. of difference	20.20 ± 10.86	28.45 ± 9.27
P	> 0.05	< 0.01

## 4.5. Biomass

### 4.5.1. Methods of estimation

Biomass estimations are the most widely used measures of the importance of populations, but there are certain difficulties in obtaining figures of biomass for Collembola. These are as follows:

i. Direct weighing is impossible for many groups as in the live state the individuals possessing a furcula cannot be handled conveniently; weighing of preserved material is practically impossible, due to the retention of the liquid preservatives in and between separate individuals.

ii. Different species are represented by individuals in various stages of development and calculations based only on the weights of adults would provide a gross over-estimate.

iii. Varying proportions of species of different sizes occur on the various sampling sites, so that it is not practicable to determine the weight of an 'average individual', and apply this to all sampling areas on different dates.

Ideally the biomass of all instars of all species present should be known before an estimate of the total biomass is made. However, this is clearly impracticable, and in practice a 'best estimate' has to be made.

MACFADYEN (1952) estimated biomass in Collembola by measuring the volume of individual adults and multiplying this by a conversion factor obtained from direct weighing of selected adults; however, it is stressed that these figures only indicate the order of magnitude of the biomass. During the course of the present work it was decided to obtain biomass figures which were as accurate as possible for one or two species, and to estimate total biomass from these. On the Limestone grassland *Onychiurus procampatus* and *Onychiurus tricampatus* accounted for approximately half of the total biomass. This estimate was made by observing the surface area covered when individuals of these two species were floated on water; it was approximately equal to that covered by the rest of the Collembola on all sampling dates.

### 4.5.2. Weights of different instars

It has been shown that the head capsules of the first six instars of *Onychiurus procampatus* are equal in size to the head capsules of the first six instars of *Onychiurus latus* (HALE 1965b). Not surprisingly the weights of the equivalent instars are also similar; 10 first instars of *Onychiurus procampatus* were found to be the same weight as 100 first instar *Onychiurus latus*; no second instars were weighed, but ten individuals of each of the other four instars were found to be similar in weight in the two species. These data are shown in Table 17.

Table 17 Comparison of the weights, in microgrammes, of different instars on *Onychiurus procampatus* and *Onychiurus latus*

Instar	1	2	3	4	5	6	7
<i>Onychiurus procampatus</i>	8.3*	—	18.0†	37.8†	83.1†	101.0†	—
<i>Onychiurus latus</i>	8.3*	—	18.0†	36.9†	82.5†	110.0†	314.4†

\* Mean of 100 individuals

† Mean of 10 individuals

The data for *Onychiurus latus* were plotted graphically (Fig. 8) and the average weight of each instar read from the graph. No direct weighings were made of individuals of *Onychiurus tricampatus*, and the assumption was made that individuals of equivalent head

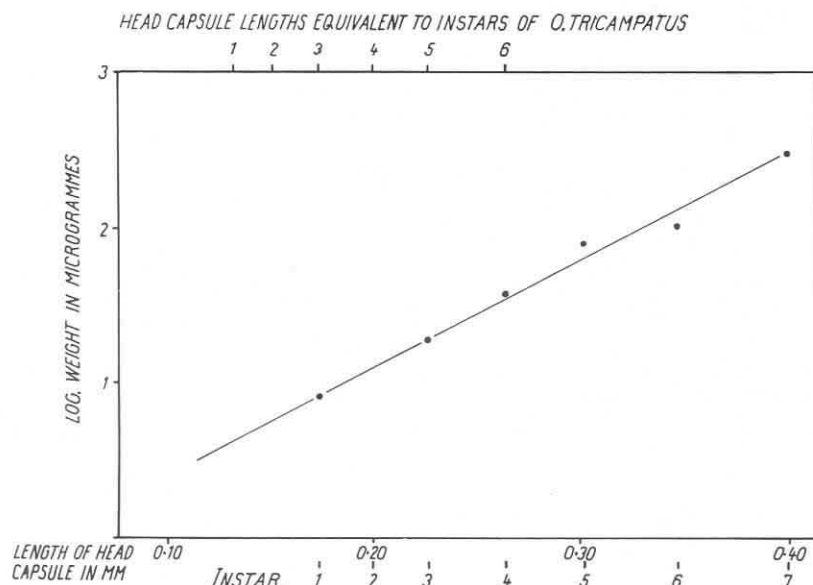


Fig. 8. The relationship between the head capsule length and the weight in *Onychiurus latus* and *Onychiurus tricampatus*.

capsule size would be equivalent in weight. Extrapolation of the graph thus gave estimates of the weights of individuals having head capsule sizes equivalent to instars one and two of *Onychiurus tricampatus*. Table 18 gives the calculated average weights of different instars from Fig. 8.

Table 18 Calculated average weights, in microgrammes, of different instars of *Onychiurus procampatus* and *Onychiurus tricampatus*

Species	Instar							
<i>Onychiurus procampatus</i>			1	2	3	4	5	6
<i>Onychiurus tricampatus</i>	1	2	3	4	5	6		
Weight per individual in microgrammes	4.2	5.6	8.3	12.6	18.0	35.5	63.1	114.8

#### 4.5.3. Biomass of the population of *Onychiurus procampatus* and *Onychiurus tricampatus*

From a knowledge of the age distribution of *Onychiurus procampatus* and *Onychiurus tricampatus* (HALE in press) and a knowledge of the average weights of different instars (Table 18), the biomass of the two species was calculated for different sampling dates. This is shown in Fig. 9. As would be expected the largest biomasses occur in early winter, at the end of the breeding season.

From these data estimates of the total biomass of Collembola on the various sampling dates can be made. It is stressed that these estimates are only approximations to the total biomass of Collembola, as it is assumed that *Onychiurus* spp. account for half the total biomass on all occasions. Table 19 gives the data for maximum and minimum biomasses on different sampling sites. The highest population density recorded of  $230,000 \pm 28,400$



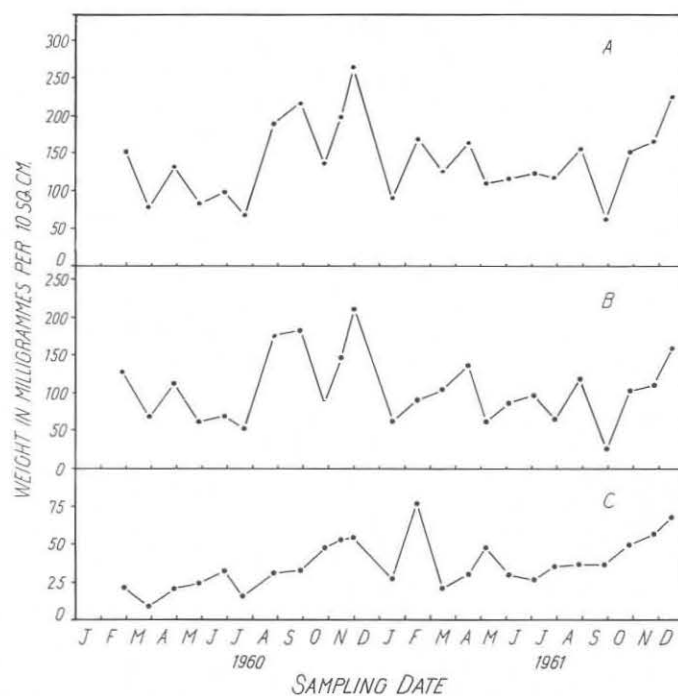


Fig. 9. Biomass, in milligrammes per ten square centimetres, of *Onychiurus* spp. on Limestone grassland during 1960 and 1961. A. *Onychiurus procampatus* and *Onychiurus tricampatus* combined; B. *Onychiurus procampatus* C. *Onychiurus tricampatus*.

individuals per m<sup>2</sup> on an area of hagg lip, on 4 December 1961, represented a biomass of about 2.53 g/m<sup>2</sup>. It can thus be seen that the biomass estimates in this work are appreciably smaller than those of BORNEBUSCH (1930) and MACFADYEN (1952, 1957).

Table 19 Maximum and minimum estimates of biomass on the four main sampling sites, in grammes per square metre

Sampling site	Maximum	Minimum	Average
Limestone grassland 1960	0.53	0.13	0.33
Limestone grassland 1961	0.45	0.13	0.29
Alluvial grassland 1960—1961	0.54	0.19	0.37
Heather litter 1961	0.47	0.10	0.29
<i>Juncus squarrosus</i> grassland 1961	0.24	0.06	0.15

#### 4.5.4. The relative importance of *Collembola* in the soil

On the basis of data provided by the present writer, CRAGG (1961) has compared *Collembola* with other groups of moorland soil animals, with respect to biomass and respiration. A biomass of 0.6 g/m<sup>2</sup> (this figure is to be regarded as a maximum) accounts for 0.3% of the total biomass on Limestone grassland, and a biomass of 0.1 g/m<sup>2</sup> accounts

for 0.1 % of the total biomass on *Juncus squarrosus* grassland. Calculations based on the respiratory determinations of BORNEBUSCH (1930) show that on these two areas 1.1 mg and 0.3 mg of oxygen are respired per square metre per hour at 13 °C by Collembola; this accounts for 2.0 % and 0.3 % respectively of the total respiration.

CRAGG (1961) points out that it is dangerous to make too detailed a comparison between the estimates of metabolic activity, since the respiratory rates of the animals under natural conditions are not known. Even so, it is clear that Collembola play a smaller part at high altitudes than is suggested by the theoretical example for a meadow soil constructed by MACFADYEN (1957), where Collembola account for 6.4 % of the total biomass and 15.2 % of the total metabolism in calories. CRAGG (1961) has pointed out that this is largely due to the relative absence of earthworms and enchytraeids in MACFADYEN'S example. It thus appears that Collembola play a smaller part in the general soil turnover on high-altitude moorland than their numerical abundance would suggest.

## 5. Discussion

Whilst it was not expected at the outset that the results of this work would show very great differences between upland and lowland populations of Collembola, certain important results have been obtained. The population densities recorded in this work are appreciably higher than those recorded by other authors for similar lowland areas (HALE in press), but to some extent this may be due to the more efficient extraction techniques used. On the other hand biomass estimates are appreciably lower than for lowland areas, and whilst to some extent this may be due to the very rough estimates of biomass that have been made in previous work, it is, at least partially, a real phenomenon. The species of Collembola occurring in upland areas tend to be the smaller species, and thus a smaller biomass is to be expected in populations of a similar size.

This work agrees with the arctic studies of AGRELL (1941) and HAMMER (1944), in that most species of Collembola were found to have only one generation a year. In lowland areas FOLSOM (1916) has recorded four generations a year in *Hypogastrura armata* (NICOLET 1841) and DAVIDSON (1934) the same number in *Sminthurus viridis* (LINNÉ 1758). Where more generations occur in a year, the contribution of Collembola to the soil turnover is greater, since more individuals are dying in a given time. The annual contribution of Collembola at high altitudes is in this way smaller than in lowland areas. It has been suggested by the present writer (HALE 1965), that high altitude Collembola possess a physiological mechanism for remaining active at low temperatures that lowland forms do not possess. In this way they may contribute more to the soil at high altitudes than do other groups, simply by remaining active.

On the relatively dry heathlands Collembola contribute to humus production through the accumulation of faecal material. Probably the best known 'coprogenous' soil is the Alpine Pitch Rendzina of KUBIENA (1953, 1955). The study area in the present work had an average annual rainfall of over 70 in (178 cm), and the soil was therefore subject to leaching. Under these circumstances the rate of accumulation of collembolan faeces must be very small (CRAGG 1961). It would be interesting to see if a coprogenous soil could be manufactured artificially on the type of blanket peat on which much of the present work was done, by lowering the water table in the way suggested by KUBIENA (1955).

In upland areas, on peat soils, the relative importance of Collembola is increased by the absence of earthworms, but, as has already been pointed out in the discussion of biomass, Collembola play a much smaller part in the moorland ecosystem than their numerical abundance would suggest. However, it may well be that the quality of their contribution may be of much greater importance than the quantity of material that they turn over.

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## 7. Summary

Collembola collected in monthly soil samples from four vegetation types (Limestone grassland, Alluvial grassland, *Juncus squarrosus* grassland and Heather litter) on the Moor House National Nature Reserve, Westmorland (1840 ft O. D., 560 m O. D.), have provided information on moorland populations.

As in lowland areas, Collembola were found to be distributed non-randomly, and aggregations were found in all the soil types studied. Inter-specific aggregations occurred, probably in areas of food concentration. Studies on the vertical distribution of Collembola in the 0–3 cm and 3–6 cm layers, on mineral soils, showed a close correlation between 'Life forms' (GISIN'S 1943 'Lebensformen') and the vertical distribution. There was a higher proportion of Collembola in the lower of the two layers in early summer and in winter, i. e. in periods of adverse weather conditions. This is probably the result of a vertical migration due to adverse weather conditions in the upper layers of the soil, but it is possibly the result of a differential mortality, or both.

Seasonal variations in numbers showed early summer and early winter peaks in total numbers of Collembola on Limestone grassland in both 1960 and 1961 and early summer peaks were also present on Alluvial grassland in 1960 and Heather litter in 1961. Analysis of the peaks occurring in three monthly running means of the data for single species suggests an annual cycle which can be correlated with egg laying periods in the field.

Limestone grassland supports a higher average population density (52,920 per m<sup>2</sup>) than Alluvial grassland (43,690 per m<sup>2</sup>), Heather litter (35,170 per m<sup>2</sup>) and *Juncus squarrosus* grassland (20,930 per m<sup>2</sup>). From the point of view of the species spectrum in each soil type, the rarer species were the better indicators of the two mineral soils: *Tullbergia affinis*, *Tetracanthella wahlgreni* and *Folsomia quadrioculata* characterised the Limestone grassland and *Hypogastrura denticulata*, *Tullbergia denisi*, *Folsomia litsteri*, *Entomobrya nicoleti* and *Lepidocyrtus lignorum* occurred more frequently on the Alluvial grassland. *Tetracanthella wahlgreni*, *Folsomia brevicauda*, *Wilowsia buski* and *Tomocerus minor* characterised the Heather litter and *Isotoma antennalis*, *Isotomurus palustris* and *Lepidocyrtus cyaneus* were characteristic of the *Juncus squarrosus* grassland site. No differences were found in and around the rosettes of *Juncus squarrosus*, but on the Heather moor *Folsomia brevicauda* was found to be associated with patches of *Sphagnum rubellum*, and *Tetracanthella wahlgreni* with patches of *Cladonia* spp.

Biomass measurements on different instars of *Onychiurus latus*, *Onychiurus procampatus* and *Onychiurus triampatus* are given and estimates are made of the average annual biomass of total Collembola on Limestone grassland (0.31 g/m<sup>2</sup>), Alluvial grassland (0.37 g/m<sup>2</sup>), Heather litter (0.29 g/m<sup>2</sup>) and *Juncus squarrosus* grassland (0.15 g/m<sup>2</sup>).

## 7. Zusammenfassung

Eine Untersuchung von Collembolenmaterial aus monatlichen Bodenproben von vier Vegetationstypen (Grasland auf Kalksteinbraunerde, Anewiesen, *Juncus-squarrosus*-Grasland auf Anmoor, Heide auf einem dystrophen Torfranker) im Moor-House-National-Naturschutzgebiet Westmorland (560 m ü. M.) erbrachte Informationen über die Populationsdynamik dieser Tiergruppe.

Wie in Niederungsgebieten, wurde eine nichtzufällige Verteilung der Collembolen beobachtet und nestartige Ansammlungen (Aggregationen) wurden in allen untersuchten Bodentypen gefunden. Interspezifische Aggregationen finden sich wahrscheinlich in Bereichen von Nahrungsanhäufungen. Studien der Tiefenverteilung von Collembolen in den oberen Bodenschichten (0 bis 3 und 3 bis 6 cm) von mineralischen Böden zeigen eine enge Beziehung zwischen Habitat und „Lebensform“ (sensu GISIN 1943). Im Frühsommer und im Winter, d. h. unter ungünstigen Witterungsbedingungen, fand sich in der tieferen der beiden untersuchten Schichten ein dichter Collembolenbesatz. Dies ist wahrscheinlich das Ergebnis einer Vertikalwanderung infolge ungünstiger Witterungsbedingungen, die sich besonders in den oberen Bodenschichten auswirken; aber möglicherweise ist diese Erscheinung auch die Folge einer unterschiedlichen Sterblichkeitsquote oder gar beides.

Der jahreszeitliche Massenwechsel zeigt Fröhsommer- und Wintermaxima des totalen Collem-bolenbesatzes im Grasland auf Kalksteinbraunerde (sowohl 1960 als auch 1961) und Fröhsommer-maxima auch in den Auewiesen (alluviale Graslandböden) im Jahre 1960 und in der Heide (1961). Eine Analyse der Maxima, wie sie sich aus den gleitenden Mitteln für jeweils drei Monate ergibt, läßt für einzelne Arten einen Jahreszyklus vermuten, der mit den Legeperioden im Freiland in Beziehung gebracht werden kann.

Die Kalksteinbraunerde unter Grasland besitzt eine höhere durchschnittliche Besatzdichte (52.920 per m<sup>2</sup>) als die Auewiesen (43.690 per m<sup>2</sup>), das Heideland (35.170 per m<sup>2</sup>) oder die Juncus-squarrosus-Wiesen (20.930 per m<sup>2</sup>). Im Hinblick auf das Artenspektrum in den verschiedenen Bodentypen sind die seltenen (rezedenten) Arten bessere Indikatoren der beiden Mineralböden: *Tullbergia affinis*, *Tetracanthella wahlgreni* und *Folsomia quadrioculata* charakterisieren die Kalksteinbraunerde unter Grasland, dagegen kommen *Hypogastrura denticulata*, *Tullbergia denisi*, *Folsomia litsteri*, *Entomobrya nicoleti* und *Lepidocyrtus lignorum* häufiger in den Auewiesen vor. *Tetracanthella wahlgreni*, *Folsomia brevicauda*, *Willowsia buski* und *Tomoverus minor* charakterisieren die Heidestreu und *Isotoma antennalis*, *Isotomurus palustris* und *Lepidocyrtus cyaneus* waren für den Standort mit *Juncus squarrosus* kennzeichnend. Keine Unterschiede wurden in Proben aus den Rosetten von *Juncus squarrosus* gegenüber Proben aus ihrer unmittelbaren Umgebung gefunden. In Heidemoor fand sich jedoch *Folsomia brevicauda* in Gemeinschaft mit *Sphagnum rubellum* und *Tetracanthella wahlgreni* in Lagern von *Cladonia spec.*

Maßangaben über die Biomasse von verschiedenen Entwicklungsstadien der Arten *Onychiurus latus*, *O. procampatus* und *O. tricampatus* werden gemacht und es wurden Schätzungen der durchschnittlichen jährlichen Biomasse des vollständigen Collem-bolenbesatzes auf Kalksteinbraunerde-Grasland (0,31 g/Mm<sup>2</sup>), Auewiesen (0,37 g/m<sup>2</sup>), Heidestreu (0,29 g/m<sup>2</sup>) und Juncus-squarrosus-Grasland (0,15 g/m<sup>2</sup>) durchgeführt.

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